



Original research article

Using climate and a minimum set of local characteristics to predict the future distributions of freshwater fish in Ontario, Canada, at the lake-scale

Brie A. Edwards^{a,b,*}, F. Meg Southee^a, Jenni L. McDermid^a^a Wildlife Conservation Society Canada, 344 Bloor St. W., Suite 204, Toronto, ON M5S 3A9, Canada^b Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

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ABSTRACT

Aim:

In order to overcome data limitations on predicting future distributions of freshwater fishes at the lake scale, our aim was to build simple species distribution models for three focal fishes from warm-, cool- and cold-water guilds, using a small set of local environmental variables paired with climate information.

Location:

A total of 6715 inland freshwater lakes across Ontario, Canada.

Methods:

Multiple logistic regression techniques were employed to model historical species occurrence with seven candidate local environmental variables, including a climate index. Model accuracy was tested by: (i) validating with a subset of the historical dataset (centered around the 1970s), and (ii) predicting species occurrence in lakes using a contemporary dataset (centered around the 2000s), representing ~30 years of climatic change. Projected climate data was then used to model species occurrence into the 2041–2070 time period.

Results:

The models for each thermal guild performed well (average AUC of 0.79) using the historical validation dataset as well as the contemporary dataset. The final set of predictors was unique to each species; however lake surface area, and the climate index were significant in all models. In all three models, the climate index was the most influential variable. Cold-water lake whitefish and cool-water walleye are predicted to be lost from a large number of lakes (1283 and 1792, respectively) by 2041–2070 across central and southern Ontario. Nevertheless, numerous hospitable lakes will be available to both fishes in Ontario's far north (OFN), where 108 lakes are predicted to be suitable for lake whitefish and 247 are predicted to be suitable for walleye. Thousands of lakes across Ontario are predicted to be hospitable for rock bass in the future, including 35 locations in OFN.

Main Conclusions:

Modified logistic regression models, incorporating a minimum of local environmental and climate information, show promise in predicting the future distributions of fishes in

* Corresponding author at: Wildlife Conservation Society Canada, 344 Bloor St. W., Suite 204, Toronto, ON M5S 3A9, Canada.
E-mail address: bedwards@wcs.org (B.A. Edwards).

Ontario lakes. This is an important first step in building conservation capacity for freshwater fishes in northern regions, where conservation value is very high, but data are particularly limited.

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1. Introduction

Climate change is widely viewed as the single greatest threat to both humans and natural systems in the next century (IPCC, 2014). Accordingly, an increasing proportion of ecological, environmental, and conservation research is aimed at understanding how climate shapes our biosphere, and how changes in climate will affect the distribution and persistence of biodiversity on the planet in the future (Felton et al., 2009; Pettoirelli, 2012).

Decades of improvements in climate modeling have yielded global and regional climate change projections with fine spatial resolution and a great deal of support from the expert academic community (IPCC, 2007, 2013). There is a consensus among scientists that climate change has already taken place, particularly at northern latitudes (Schindler, 2001; Colombo et al., 2007; Rusak et al., 2008; IPCC, 2013; Alofs et al., 2013), and that ongoing changes will occur at an accelerated pace in the years to come (IPCC, 2013). In the northern hemisphere, warming over the past 30 years is unequivocal, and each successive decade has been warmer at the earth's surface than anything observed since 1850 (IPCC, 2013). Predictions for the future include air temperature increases, altered precipitation patterns, and an increase in the frequency of extreme climatic events (IPCC, 2007, 2013). Because changes in climate are projected to be most intense at higher latitudes, northern taxa that are cold-climate specialists are expected to be among the most negatively impacted by climate change.

Freshwater systems are currently among the most threatened on the planet (Allan and Flecker, 1993; Dudgeon et al., 2006; Abell et al., 2011), and they face particularly intense climate change impacts, in conjunction with multiple additional stressors (Schindler, 2001; Keller, 2007). In lakes, climate change will lead to altered thermal characteristics, increased durations of ice-free seasons, and changes in water levels (Magnusson et al., 1997; Keller, 2007; Rusak et al., 2008). These environmental changes will alter the quality and quantity of habitat for fishes and other lake inhabitants (Keller, 2007; Lynch et al., 2016). At a broad scale, fish thermally adapted to cold waters are predicted to lose habitat at the southern edges of their range, where they may be unable to escape warm waters (Abell, 2002; Shuter et al., 2002; Minns et al., 2009; Gunn and Snucins, 2010; Shuter et al., 2012). Cool- and warm-water fishes are predicted to expand northward as new lakes become suitable beyond their current northern range limits (Magnusson et al., 1997; Chu et al., 2005; Keller, 2007; Alofs et al., 2013). Such expansions may impose additional stress on native cold-water species due to increased competition and predation (Vander Zanden et al., 1999; Jackson and Mandrak, 2002; Sharma et al., 2011).

The province of Ontario, Canada spans a large latitudinal range and contains approximately 250,000 inland lakes. Over 30,000 of these lakes are located north of the commercial limit to forestry, in what is known as Ontario's far north region (OFN), a vast and relatively undeveloped landscape. Unfortunately, little is known about the physical characteristics of the majority of these northern lakes, or the fish communities they contain. In fact, numerous researchers in Canada have identified a disparity of both physical and biological knowledge of northern lakes across the country (Chu et al., 2003; Minns et al., 2008; McDermid et al., 2015a). Climate studies project that OFN will warm significantly over the next century (greater than 10 °C in some areas) and experience altered seasonal precipitation (Colombo et al., 2007; Vincent et al., 2012; McDermid et al., 2015b). Both trends have already been detected in observational data (Magnusson et al., 1997, 2000; Schindler, 2001; Alofs et al., 2013).

Regional-scale evaluations of future climate suitability predict northward range expansions of warm- and cool-water sport fish in Ontario (Vander Zanden et al., 2004; Chu et al., 2005; Sharma et al., 2009). Despite concern that freshwater species might have a limited capacity to adapt to climate changes, due to the insular nature of freshwater habitats (Strayer and Dudgeon, 2010), such northward expansions are already being documented in lakes (Alofs et al., 2013).

Over the last century, humans have been altering the distributional patterns of numerous bait and sport fishes across Ontario, via the intentional or unintentional movements of individuals related to fishing activities (Sharma et al., 2009; Alofs et al., 2013; Drake and Mandrak, 2014), as well as the direct effects of fishing pressure. Various indicators of human use intensity, including population size, road density, or estimates of 'attractiveness' for recreational activities, have been linked with the likelihood of human mediated dispersal of fishes among inland lakes (Drake and Mandrak, 2014; Leathwick et al., 2016). Human mediated dispersal is likely to play a role in future range shifts related to changes in climate suitability (Alofs et al., 2013) and at the lake scale proxies of human use may be an important predictor of occupancy.

Additionally, making specific predictions as to which lakes will be hospitable to individual fish species in the future, under various climate change scenarios, requires the inclusion of important lake habitat characteristics into species distribution models (Jackson et al., 2001). The local climate interacts with aspects of lake size, depth and shape to determine the relative availability of different thermal habitats, and therefore the effects of climate change on species with different thermal preferences will be non-uniform within climatic regions based on variability in lake morphology (Minns, 1989; Minns et al., 2009; Minns and Shuter, 2013; reviewed in Lynch et al., 2016). Also, depending on the range of climate conditions

represented by the sampled region relative to the thermal tolerance range of focal species, the relationship between climate and occupancy captured may be increasing, decreasing, or bell-shaped (Minns and Moore, 1995).

Predicting distributional changes of freshwater fishes at the local lake-scale is fraught with difficult complexities, but without such estimates, planners and policy makers are unable to make specific recommendations for the conservation of freshwater fishes in these waters. For instance, identification of lakes with high conservation potential for cold-water adapted native fishes could be incorporated into spatial planning under the province of Ontario's commitment to protect 50% of OFN under Ontario's [Far North Act \(2010\)](#).

While our study was in review, an article was published that provides the only other study we are aware of attempting to predict lake occupancy of several fishes in Ontario under climate change at the lake scale (Van Zuiden et al., 2016). Using smallmouth bass, walleye, and cisco, Van Zuiden and co-authors found that the lake occupancy of each thermal representative could be modeled using logistic regression and a unique combination of summer air temperatures and precipitation levels along with lake size, depth and water clarity. The emergence of their work provides an exciting opportunity for comparison with our approach, which includes a number of additional considerations and two unique focal species.

In this study we evaluate whether the relationship between focal species occupancy and climate in Ontario lakes is best described by simple one-directional or bell-shaped logistic curves, and then assess the potential for interactive effects between local climate and lake depth. We further include a consideration of overall lake shape, as well as the potential influence of human use intensity on occupancy patterns.

The specific objectives of this study were: (1) to use historical data from lakes across Ontario to generate species distribution models for a focal fish species from each thermal guild (warm-, cool-, and cold-water), that perform well when climate and a small set of important morphological characteristics, along with a proxy for human use intensity, are included as predictors; (2) to determine whether these models can accurately predict occupancy over a recorded period of climate change, using contemporary occurrence and climate data that span an approximately 30-year interval; and (3) to predict future distributions of our focal species using 'business as usual' climate projections for the 2041–2070 time period.

2. Methods

2.1. Model inputs

2.1.1. Fish community and lake attribute data

Historical fish occurrence records for Ontario were obtained from a database of >7000 lakes (hereafter referred to as 'historical') that was contributed by the Ontario Ministry of Natural Resources and Forestry (OMNRF). All records were collected as part of the Aquatic Habitat Inventory program between 1958 and 1995 (Dodge et al., 1985). Of these records, 6747 lake records could be positively identified and located on an up-to-date GIS layer of Ontario waterbodies (Ontario Hydro Network—Waterbody; OMNRF, 2015). A further 32 records contained errors or omissions, thus the final historical dataset contained 6715 lake records from 128 tertiary watersheds, although 27 of these watersheds were represented by 5 or fewer lakes.

A contemporary fish occurrence and lake characteristic dataset (hereafter referred to as 'contemporary') was also provided by the OMNRF. This dataset consisted of 745 lake records from Ontario, which were sampled as part of the Broad-scale Monitoring program between 2007 and 2012 (Sandstrom et al., 2010). Forty-eight of the records had errors or missing data, resulting in a final dataset of 697 lakes for use in analyses. A large number of the contemporary lakes (546) had also been sampled as part of the historical surveys.

A fish species from each thermal guild (warm-, cool- and cold-water) was selected for this study. Rock bass, *Ambloplites rupestris*, was selected as our focal warm-water species. Rock bass is a centrarchid fish that is native to the Ohio River and lower Great Lakes basins, but has been expanding its distribution northward in Ontario over the past century via human mediated dispersal (Scott and Crossman, 1973; Alofs et al., 2013; Eakins, 2014). There is evidence that warm-water centrarchids pose a threat to native species in the systems they invade (Jackson and Mandrak, 2002; Vander Zanden et al., 2004; Pease and Paukert, 2014). Furthermore, it was recently found that rock bass have invaded a greater number of lakes than either smallmouth or largemouth bass (Alofs and Jackson, 2015b). Walleye, *Sander vitreus*, was selected as our focal cool-water fish. Walleye is present in lakes throughout Ontario and is highly sought after for commercial and recreational fishing as well as subsistence fishing in northern communities (Scott and Crossman, 1973; Eakins, 2014). Finally, lake whitefish, *Coregonus clupeaformis*, was selected as our focal cold-water fish. Whitefish has both a northern and southern range-limit in Ontario, and is also very important for recreational and subsistence fishing in OFN (Scott and Crossman, 1973; Eakins, 2014). We are not aware of any previously documented contemporary changes in the Ontario ranges of walleye or lake whitefish.

Our intention was to use lake characteristic data that lacked omissions and could predict species occurrence with high accuracy while using as few variables as possible. Therefore, we considered six variables in our analyses, including lake area ('AREA', ha), maximum depth ('MAXD', m), mean to maximum depth ratio ('DRATIO'), water clarity as estimated by secchi depth ('SECC', m), lake elevation ('ELEV', m above sea level), and the density of buildings present ('BLDGD', n/shoreline km). Depth ratio, which provides a useful approximation of lake shape (Carpenter, 1983; Minns et al., 2009), along with

lake area and maximum depth, are all determinants of the relative availability of various types of habitat and thus tend to have strong relationships with fish occurrence (Minns, 1989; Jackson et al., 2001). Water clarity is a proxy for overall lake productivity as well as visibility conditions, which is important because fish species vary in terms of their visual light sensitivities and reliance on sight for detection of food resources (Scott and Crossman, 1973). Lake elevation is often linked to lake connectivity, and therefore accessibility for invasion through natural pathways, because higher elevation lakes tend to be more isolated within the watershed network (Minns, 1989; Olden et al., 2001).

2.1.2. Human development data

The density of buildings present around the perimeter of the lakes (n/shoreline km) was included as an indicator of human use intensity. Historically, building counts were made during a boat cruise around the shoreline, at which time a surveyor would count the number of commercial establishments (termed 'resorts', Dodge et al., 1985) and the number of private residences, cottages or cabins (termed 'cottages', Dodge et al., 1985). We assumed that this visual survey from shore would have captured buildings present within 50 m of the lake perimeter. For the contemporary lake surveys, field assessments of building count were not conducted, and so this information was derived from a number of GIS layers obtained from the OMNRF. Subsets of the following datasets were used to derive a more accurate representation of the number of buildings within 50 m of the shoreline: Building as Symbol, Recreation Point, Cottage Residential Site, Recreation Camp, and Tourism Establishment Area (OMNRF, 2015). The number of private or commercial buildings within a 50 m buffer around the lake polygon was extracted from each data layer and then combined to produce a single count for each lake.

For each lake in the larger historical dataset, we generated a contemporary count of the number of buildings present within 50 m of the shoreline, using our GIS approach, for use in our projections for the 2041–2070 period. The number of buildings was either unchanged or increased in the majority of lakes between historical and present-day, however a small number of lakes had a reduction in count, indicating an area of weak GIS coverage in our building layers, or an area of population decline. In these cases we used the historical densities in our projections as an indication of realistic potential development intensity.

2.1.3. Climate data

We obtained downscaled, 10 km resolution, climate grid data from the Canadian Forest Service (CFS), which had been generated using a thin plate spline-smoothing algorithm (McKenney et al., 2006, 2011, 2013). A baseline model average of the 30-year period spanning 1961–1990 was used to accompany the historical fish occurrence records. A baseline model average of the 30-year period spanning 1981–2010 was used to accompany the contemporary records.

Climate projection grids for the period spanning 2041–2070, produced by the Canadian Coupled Global Climate Model 3.1 (CGCM31R) based on the 4th IPCC assessment report (2007), were obtained from the CFS similarly downscaled to ~10 km resolution. The model was run using the A2, "business as usual" scenario, which predicts a continuation of current trends in greenhouse gas emissions (IPCC, 2007).

The obtained climate grids included minimum and maximum July air temperature (°C), minimum January air temperature (°C), annual precipitation (mm), and the estimated Julian dates of lake ice out (date when ice coverage becomes incomplete) and lake ice in (date when ice coverage becomes complete). Lake ice in/out dates were generated by the CFS using a multiple regression model based on average spring and fall air temperatures (detailed in Williams et al., 2004; McKenzie et al., 2013). Lake ice out date was subtracted from lake ice in date to obtain a grid layer of the ice-free duration (days).

Values of our four climate variables (ice-free duration, mean July air temperature, minimum January air temperature, and total annual precipitation) were extracted at the location of each lake by averaging the values of all grid cells overlapping the lake polygon.

All climate data was processed and extracted using ArcGIS 10.2 (ESRI, 2015).

The four climate variables we selected for use in our models were highly positively correlated, so Principal Components Analysis (PCA) was utilized in order to reduce the climate information down to a smaller set of independent variables. A single PCA was conducted that included all three lake datasets (historical, contemporary, and future) in order to capture the full range of temporal climate variation. The first PCA axis, which explained 78% of the total variance, was the only one deemed significant using a broken stick analysis (Jackson, 1993), and was highly positively associated with all four climate variables. Lake site scores on PCA axis 1 were used as a single climate index variable ('CLIM') in our species distribution models.

Fish species yield and occurrence follows a bell shaped curve over its range of thermal tolerance (Minns and Moore, 1992, 1995). Depending on the sampled range, one side of the relationship (increasing or decreasing) may be captured, which would be fit effectively using simple logistic regression. However, if more of the thermal range is covered, the relationship may be improved by adding a quadratic term to allow for a bell shaped fit (Minns and Moore, 1995). Logistic regression of historical occupancy along the CLIM gradient revealed that, consistent with previous work in Ontario (Minns and Moore, 1995), the bell shaped curve improved the fit for lake whitefish and walleye (see Supplement A for regression summaries and fit plots), but not rock bass. Therefore, a quadratic climate index term (CLIM²) was incorporated into the modeling for these two focal species.

Table 1

Summary information for all candidate variables in the historical dataset, and final species distribution models, including the regression coefficients, odds ratios, and statistical significance for each retained variable.

Candidate variables	Range			Lake whitefish			Walleye			Rock bass		
	Min	Max	Mean	Coef	Log Ratio	p	Coef	Log Ratio	p	Coef	Log Ratio	p
AREA	0.20	140 943	488.27	0.0005	1.0005	< 0.001	0.0008	1.0008	< 0.001	0.0001	1.0000	0.021
MAXD	0.60	213.50	18.46	0.0457	1.0467	< 0.001	0.0029	1.0029	0.509	0.0207	1.0209	< 0.001
DRATIO	0.03	1.00	0.35	−0.7794	0.4587	0.026	−0.6170	0.5398	0.051			
ELEV	0.00	875.00	337.43				−0.0054	0.9946	< 0.001	−0.0070	0.993	< 0.001
SECC	0.00	36.60	3.60	−0.1128	0.8933	< 0.001	−0.2910	0.7475	< 0.001	−0.0154	0.9847	0.512
BLDGD	0.00	90.99	0.80				0.0959	1.1007	< 0.001	0.0735	1.0762	< 0.001
CLIM	−5.95	2.62	−1.18	−0.9699	0.3791	< 0.001	−1.1760	0.3084	< 0.001	0.3870	1.473	< 0.001
CLIM ²				−0.1105	0.8954	< 0.001	−0.1750	0.8395	< 0.001			
MAXD:CLIM				0.0082	1.0092	< 0.001	0.0040	1.0040	0.055			

2.2. Fish occurrence models

Historical fish occurrence in relation to lake characteristics and climate was modeled for each of our three focal species individually using multiple logistic regression. Models were trained using a random selection of 75% of the sites, and their performance was evaluated using the remaining 25% of sites as an independent validation dataset. The proportions of presences (23%, 33%, and 17% of lakes, respectively, for lake whitefish, walleye, and rock bass) were held constant when randomizing sites into the training and validation datasets.

The global model consisted of the full suite of candidate variables (lake attributes, building density and the climate index), and an ‘all subsets’ selection procedure was used to identify the 5 best performing subset models based on the Akaike Information Criteria (AIC). We further created variations of the best models with the potential interaction between MAXD and CLIM, and compared the full set of models based on AIC to select the final best model (see Supplement B for AIC ranks and weights). In instances where several top models were within $AIC < 2$, we selected the model that had the best overall performance using the validation data. The statistical significance of each variable retained in the final model was determined along with its relative importance as indicated by the raw and exponentiated regression coefficients (log-ratios) (Table 1; see Supplement C for plots of the modeled relationships between the probability of occurrence of each species and the retained variables).

Once model predictions were generated for the validation datasets, we employed a method to determine the optimal threshold value to distinguish predicted presence from absence for each species model. We opted for individual threshold determinations rather than using an *a priori* threshold because the fish occurrence data have many fewer presences than absences, which will bias the probabilities toward zero (reviewed in Wilson et al., 2005). We identified the threshold value in each model that maximized the phi coefficient of fit between model predictions and observations in the validation dataset, thereby optimizing the tradeoff between false-negative and false-positive error rates.

Overall model performance was assessed by generating receiver operating characteristic (ROC) curves for each model and then calculating the area under that curve (AUC). Sensitivity (proportion of correctly predicted presences) and specificity (proportion of correctly predicted absences) were also calculated, at the identified optimal presence/absence threshold for each model.

The final selected models produced using the historical dataset were then used to make occurrence predictions for each species in the contemporary lake dataset, using contemporary predictor data. Model performance metrics were generated by comparing the predicted probabilities to actual observed occurrences (lake whitefish, walleye, and rock bass were present in 53%, 70%, and 43% of contemporary lakes, respectively). As before, the phi coefficient was used to identify the appropriate prediction threshold, and sensitivity, specificity and AUC were calculated.

Logistic regressions were conducted in the R-language environment, version R.3.2.2, using the ‘glm’ function (R Development Core Team, 2015). The variable selection procedure was carried out using the package ‘glmulti’ (Calcagno, 2015) and performance evaluation was carried out using the package ‘ROCR’ (Sing et al., 2013).

2.3. Future occurrence predictions

To generate future occurrence predictions for each species, the fish occurrence models were used with the larger, historical set of lake characteristic data, paired with the climate index from future climate projections, and contemporary building densities.

3. Results

3.1. Climate characteristics

Ice-free duration in Ontario ranged from 135 to 260 days in the baseline period, from 141 to 264 days in the contemporary period, and from 174 to 284 days in the future projection. Minimum and maximum July air temperatures were averaged to

Table 2

Final selected model performance metrics for each species, using (a) the historical validation dataset and (b) the contemporary dataset.

	Maximum phi	Threshold p	Sensitivity	Specificity	AUC
(a)					
Rock bass	0.358	0.279	0.478	0.884	0.745
Walleye	0.468	0.359	0.743	0.746	0.811
Whitefish	0.433	0.328	0.532	0.886	0.802
(b)					
Rock bass	0.521	0.211	0.671	0.850	0.797
Walleye	0.412	0.316	0.741	0.697	0.767
Whitefish	0.543	0.248	0.861	0.669	0.836

produce a mean July air temperature grid. Mean July air temperature values for Ontario ranged from 11.5 to 22.8 °C in the historical period, 13.0 to 23.3 °C in the contemporary period, and 13.5 to 26.2 °C in the future projection. Minimum January air temperature ranged from −30.6 to −7.7 °C in the historical period, from −28.1 to −6.4 °C in the contemporary period, and from −22.7 to −2.5 °C in the future projection. Annual total precipitation ranged from 428 to 1193 mm in the historical period, 454 to 1228 mm in the contemporary period, and 493 to 1290 mm in the future projection.

3.2. Fish occurrence models

The all subsets selection procedure produced a unique set of retained variables in the final model for each species (Table 1). All variables considered were retained in at least two of the species models, and lake area and CLIM were retained and statistically significant ($p < 0.05$) for all three species. Rock bass occurrence was associated with larger, deeper lakes at lower elevations, with high building densities, and high CLIM scores. There was no interaction between the influence of CLIM and MAXD on occurrence (Fig. 1(c)). Walleye occurrence was associated with large, lower elevation lakes with lesser water clarity, where building densities were high and climate index scores were low. There was a significant interaction between CLIM and MAXD, wherein occupancy increased with MAXD where CLIM was high, but decreased with MAXD where CLIM was low (Fig. 1(b)). Lake whitefish occurrence was unrelated to building density, but was associated with large lakes with low mean:maximum depth ratios, lesser water clarity, and low CLIM scores. There was a significant interaction between CLIM and MAXD wherein occupancy increased with MAXD only where CLIM was high (Fig. 1(a)).

Model performance metrics indicated good overall performance when validating using both the historical validation dataset and the contemporary dataset (Table 2). Using the historical validation set (Table 2(a)), the walleye model had the best overall performance with an AUC of 0.81. Sensitivity and specificity were similar, at 0.74 and 0.75, respectively. Overall performance of the lake whitefish model was only slightly lower with AUC of 0.80. Sensitivity was poor for lake whitefish at 0.53, however specificity was very strong at 0.89. Performance was lowest for the rock bass model, though still fair with an AUC of 0.75. The model had very poor sensitivity at 0.48, but high specificity at 0.88.

Using the contemporary dataset for validation (Table 2(b)), the lake whitefish model performed the best (AUC of 0.84), followed by the rock bass model (AUC of 0.80) and then by the walleye model (AUC of 0.77). Relative values of sensitivity and specificity were very similar between the contemporary and historical validation procedures, with the exception of improved sensitivity in the contemporary predictions of lake whitefish (0.86) and rock bass (0.67) (Table 2(b)).

Comparison of contemporary and historical occurrences in the 546 lakes that were surveyed in both time periods allowed for an assessment of observed apparent changes in the distributions of each species (Fig. 2). Far more lake populations were apparently gained than lost for all three species, however rock bass experienced both the greatest number of apparent gains, and the fewest apparent population losses. Lake whitefish was newly detected in 77 lakes but apparently lost in 18 (net increase of 59 populations or 23.9% of historical, Fig. 2(a)) and walleye was detected in 75 new lakes, but apparently lost in 14 (net increase of 61 populations or 18.7% of historical, Fig. 2(b)), whereas rock bass were newly detected in 86 lakes and apparently lost in 5 (net increase of 81 populations or 49.7% of historical, Fig. 2(c)). Our rock bass model correctly predicted 72% of maintained populations, 60% of observed gains, and 80% of observed losses. The walleye model correctly predicted 80% of maintained populations, 52% of observed gains, and 57% of observed losses. The whitefish model correctly predicted 90% maintained populations, 77% of observed gains, and 50% observed losses.

3.3. Future occurrence predictions

Both cool-water walleye and cold-water lake whitefish are predicted to lose a large number of suitable lakes (1792 and 1283, respectively) throughout Ontario by the 2041–2070 period (Fig. 3(a), (b)). Habitat losses are most intense across the southern and central portions of their historical ranges, south of OFN. Walleye in particular show a stark contrast within OFN, where almost no losses are predicted and 247 lakes remain or become hospitable (Fig. 3(b)).

More than two thousand lakes are predicted to become suitable for the establishment of warm-water rock bass across Ontario, particularly in southern and central regions (Fig. 3(c)). Hospitable lakes appear all the way up to the northern edge of the province. There is a concentration of lakes in northwestern Ontario, just south of the line distinguishing OFN, which

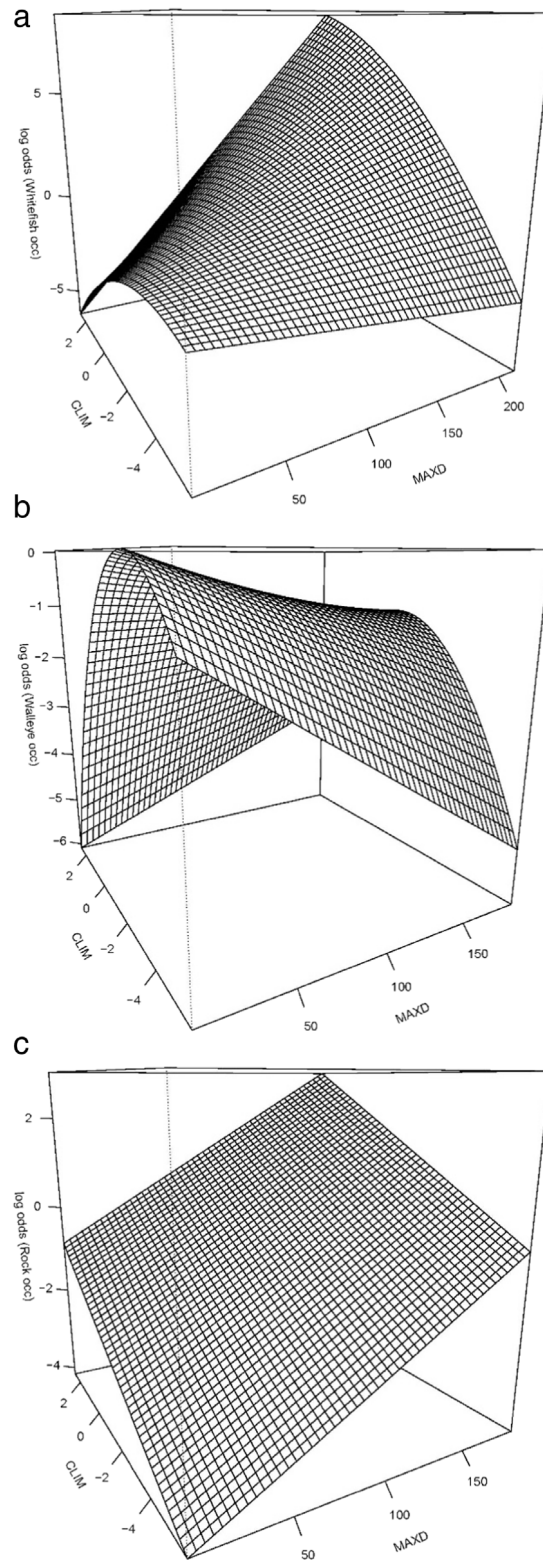


Fig. 1. Modeled three dimensional relationships between the log odds of occurrence, the CLIM index, and Maximum Depth (MAXD) for (a) Lake whitefish, (b) Walleye, and (c) Rock bass.

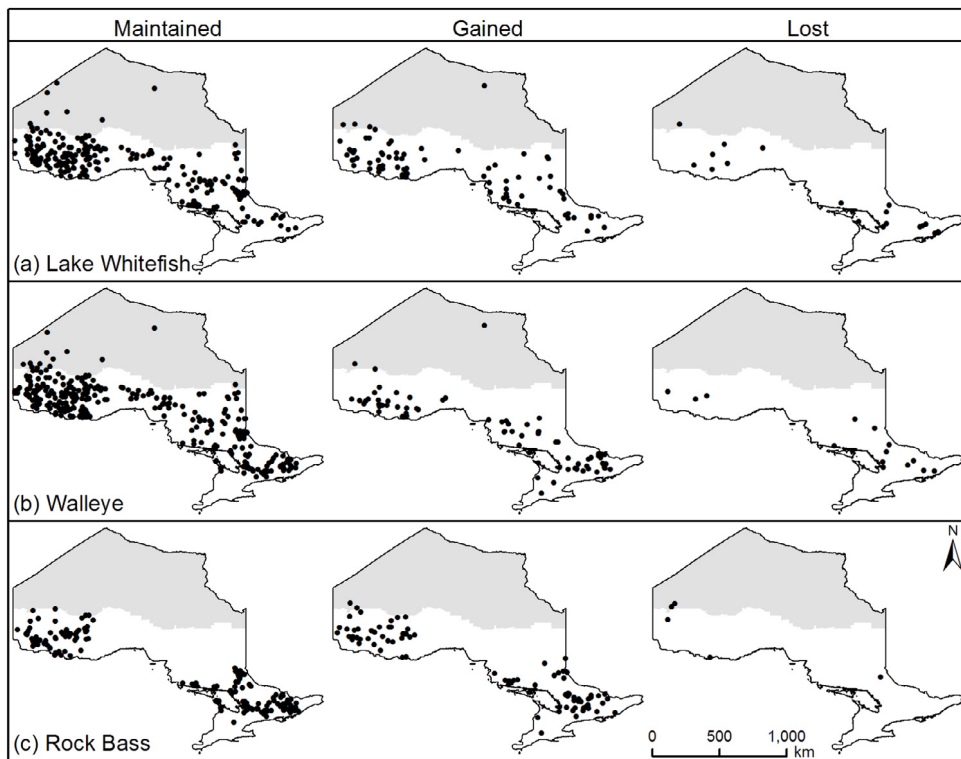


Fig. 2. Observed changes in species occurrence between the historical and contemporary surveys for (a) lake whitefish, (b) walleye, and (c) rock bass, including maintained presences (left panel), gains (center panel), and losses (right panel). The shaded region delineates OFN.

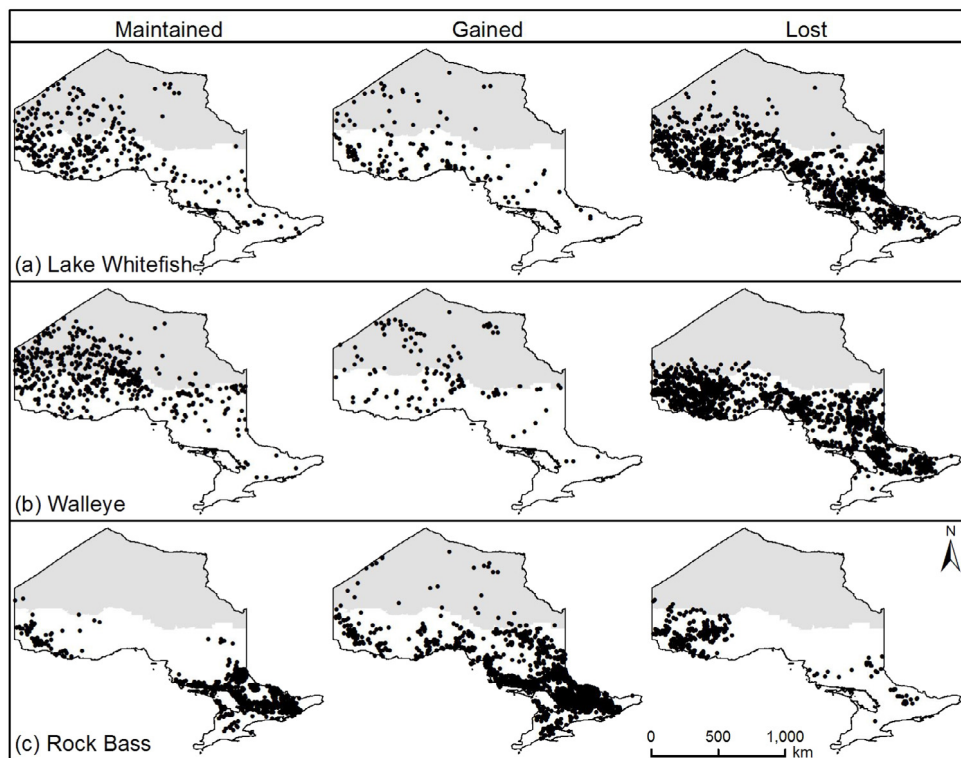


Fig. 3. Predicted changes in species occurrence between the historical survey and 2041–2070 for (a) lake whitefish, (b) walleye, and (c) rock bass, including forecasted maintained presences (left panel), gains (center panel), and losses (right panel). The shaded region delineates OFN.

are predicted to become inhospitable to the rock bass they currently contain (Fig. 3(c)). This is the same area where 4 of 5 observed population losses between the historical and contemporary surveys occurred. Overall, seventy five percent of the historical rock bass populations are predicted to be maintained.

4. Discussion

4.1. Predictors of lake occupancy

Our models performed well, with overall classification rates ranging from 0.75–0.84 depending on the species and validation time period. Specificity, or percent of correctly predicted absences, were typically fair to high (ranging from 0.67–0.89), whereas sensitivity, or percent of correctly predicted presences, ranged more widely depending on species and time period (ranging from 0.48–0.86). Both historical and contemporary validation of the rock bass model found that the model was much better at predicting absence, however there was a marked improvement in the rate of correctly predicted presences between time periods. Over-prediction of occupancy (i.e., low specificity) might be expected when an invading species has yet to become established in predictably suitable localities. As increasing numbers of suitable localities are invaded, a greater proportion of predicted occurrences would be realized, improving model specificity. Based on these aspects of performance, we feel confident that our predictions provide reliable estimates of both high and low likelihood of rock bass invasion by 2041–2070.

Similar to rock bass, lake whitefish validation indicated a marked increase in the model sensitivity between the historical and contemporary surveys, whereas the walleye model displayed fairly similar sensitivity and specificity in both time periods. Taken together, we feel confident that predictions for 2041–2070 generated by these models provide a balanced estimation of both future occurrence and potential population losses under climate change.

The logistic models produced by Van Zuiden et al. (2016) had very similar overall performance with classification rates ranging from 0.80–0.84. Their sensitivity values, however, were consistently low (ranging from 0.56–0.66) and specificity values were all high (ranging from 0.86–0.89). Unfortunately, their modeling approach replaced historical with available contemporary records, and used climate averages over 1950–2000, thereby ignoring the changes in climate and occurrence that we have documented in this study between survey periods. This also makes our model performances in either the historical or contemporary validation difficult to compare to the work by Van Zuiden et al. (2016).

The final combination of significant predictors of occurrence was unique to each species occurrence model, however, lake area was a significant predictor in all three models, and elevation was significant for both walleye and rock bass. Lake area and elevation are often inversely related, and the generally smaller lakes at the top of watersheds tend to have lower relative connectivity to the greater network as compared to larger lakes lower down, potentially limiting their accessibility for dispersal (Sorrano et al., 1999; Riera et al., 2000; Martin and Sorrano, 2006). Because lake order, or the relative position of lakes in a watershed is related to both connectivity and habitat characteristics, it has been found to play a large role in structuring aquatic communities (Minns, 1989; Olden et al., 2001; Cottenie and De Meester, 2003; Heino and Muotka, 2006).

We found that lake depth ratio had varying significance as a predictor of lake occupancy for our three fishes. Depth ratio was only retained in the lake whitefish and walleye models, and was much more important for the cold-water lake whitefish, which was associated with lower ratios, or more v-shaped basins with steeper sides. Despite its demonstrated importance in the literature as an indicator of lake shape and the relative availabilities of both cold, deep and warm, inshore habitats (Carpenter, 1983; Rasmussen and Kalff, 1987; Vadeboncoeur et al., 2008), it is possible that across the large spatial scale of this study, spanning multiple ecoregions (Crins et al., 2009), that depth ratio is a more consistent indicator of the relative availability of aquatic habitat for cold-water specialists.

Both rock bass and walleye presence were positively associated with building density, which was not a significant predictor in the lake whitefish models. Fish species used for human purposes, such as sportfish and commonly purchased baitfish, are more frequently transported by humans between waterbodies (Drake and Mandrak, 2014), and are unsurprisingly the species that have shown the greatest northward range-shift in Ontario over recent decades (Alofs et al., 2013). An association between smallmouth bass invasion and human use intensity has been shown previously (Sharma et al., 2009), and a similar pattern was recently identified for rock bass (Alofs and Jackson, 2015a). The association of walleye with building counts may indicate that walleye are more likely to be moved by humans than whitefish. The presence of walleye (or the characteristics of lakes that contain them) may also be a greater attractant for human development.

The GIS datasets obtained to generate contemporary building counts may have been inaccurate in some areas, however all of them were documented to have been updated recently, between 2006 and 2012. In the few instances where lakes appeared to lose buildings we opted to use the historical visual count in our forecast models as an indication of potential development density into the future. High rates of anthropogenic conversion of shoreline areas in Ontario shield lakes have been observed in recent decades (Molot and Dillon, 2008; Yan et al., 2008) and concerns over the ecological impacts of overdevelopment on lakes across Ontario's shield region precipitated the development of shoreline capacity models to limit development (Ontario Ministry of the Environment, 2010). It is possible that building densities will continue to increase in some areas, potentially increasing the likelihood of human mediated dispersal.

Our climate index was a significant predictor in all three fish distribution models, and was the most important driver relative to other local variables in each case. This would appear to indicate that broad scale filters such as climate are more influential than local-level abiotic factors for the three species we studied. We have further shown that simple logistic

increasing curves relating occupancy to climate conditions are appropriate for our focal warm-water species across Ontario, but that our focal cool- and cold-water species occurrence is best represented by a bell-shaped curve. Moreover, we have identified an important link between lake depth effects and climate that varies among thermal guilds. We know that when summer air temperatures are high, cold-water habitat becomes restricted to the bottom portion of deep lakes (Minns et al., 2009; Shuter et al., 2012; Minns and Shuter, 2013). Accordingly, we found that occupancy of cold-water lake whitefish in colder regions is unrelated to lake depth, but is increasingly associated with lake maximum depth in warmer regions with longer ice-free seasons. Cool-water walleye are similarly associated with deeper lakes in warm regions with longer ice-free seasons, however in cooler climates the relationship actually reverses, and occurrence is negatively associated with lake maximum depth.

Projections of future climate conditions will always be accompanied by some degree of uncertainty. At the time our climate projections were acquired from CFS, the CGCM model represented best available data, tailored to the region of interest and scaled down appropriately to capture local lake-level variability (IPCC, 2007; McKenney et al., 2011). It was not our aim to capture uncertainty in climate modeling, but rather to explore differences in the combined influence of climate and local environmental drivers among focal species using observed data, and to make baseline future predictions that can be compared with other approaches. Since our models were generated, a newer set of IPCC climate models accompanying the 5th assessment report (AR5) became available at the desired spatial scale (IPCC, 2013). Models in AR5 employ a new set of climate policy scenarios called Representative Concentration Pathways (RCPs). The most intensive of these RCPs (RCP 8.5) is a logical extension of the previous SRES A2 “business as usual” scenario used in this study because no global emission targets are set, which would more than double current greenhouse gas concentrations by 2100 (Riahi et al., 2011; Rogelj et al., 2012; IPCC, 2013). Despite differences in the underlying scenarios and technological advancements in the models employed, the trajectories of surface temperature increases under RCP 8.5 are very similar to those under SRES A2, although mean surface temperatures are generally higher under RCP 8.5 (Harris et al., 2014). The AR5 fine-scale predictions equivalent to those we used under AR4 show very similar patterns for warming and altered precipitation across northern Ontario, although the projections we used under SRES A2 are somewhat more conservative (McDermid et al., 2015b).

4.2. The potential expansion of rock bass in Ontario

Our model predicts the intensification of rock bass occupancy throughout southern and central Ontario where it already occurs, as well as numerous new populations in western and northern Ontario, which would extend their range to encompass the entirety of the province. Lake suitability for rock bass was associated with high climate index values and building densities, in large, deep lakes with low elevations. Our findings are consistent with a recent study that related invasion success for rock bass in Ontario lakes over recent years to warmer climate, greater surface area, close proximity to roads, and low elevation (Alofs and Jackson, 2015a). Validation assessments using both historical and contemporary occurrence data found that our rock bass models were far better at predicting absences (specificity) than correctly predicting presences (sensitivity), which indicates that rock bass have not yet had opportunity to become established in areas that are currently suitable.

Van Zuiden et al. (2016) similarly predicted that warm-water smallmouth bass will expand their range, however high probabilities of occurrence were only predicted for the western edge of OFN. Unfortunately, the authors did not report the optimal threshold probability to best distinguish predicted presence from absence making it difficult to interpret their projections. Furthermore, the smoothing function they used to create a probability surface masks lake-level predictions and makes it difficult to distinguish areas of low habitat suitability from areas without local information.

Alofs and Jackson (2015a) showed that Ontario lakes with historical walleye presence were 3.5 times more likely to be invaded by rock bass, which was attributed in part to intentional rock bass introductions in locations valued for native sport fishing. Furthermore, consistent with a long history of association between rock bass and smallmouth bass occupancy (Eakins, 2014), the establishment of smallmouth bass and largemouth bass was found to be more likely in lakes that have been previously invaded by rock bass (Alofs and Jackson, 2015b). In light of these findings, our predictions for future rock bass occurrence can be taken as a likely indicator of the additional establishment of smallmouth and largemouth bass, and a great potential for interactions between invading centrarchids and resident walleye populations.

Very little is known about the potential negative impacts of rock bass invasion on native fish communities. However, the impacts of smallmouth bass invasion have been more widely studied. Intense predation by smallmouth bass can lead to the extirpation of cyprinid minnows and drastic reductions in the diversity of prey fish communities (MacRae and Jackson, 2001; Jackson, 2002; Alofs and Jackson, 2015b). Smallmouth bass can out-compete lake trout in the consumption of available littoral forage fish (Vander Zanden et al., 1999), and have been observed to predate directly upon salmon fry and smolts (Harvey and Kareiva, 2005). Declines in walleye populations coincident with the introduction and establishment of smallmouth bass have been attributed to both competitive and predatory interactions (Frey et al., 2003; Wuellner et al., 2011a,b), although the type and severity of negative interactions observed have been variable (Johnson and Hale, 1977; Wuellner et al., 2011b).

It is reasonable to assume that rock bass invasion has similar impacts to those of smallmouth bass, because both fishes are considered benthic-pelagic invertivore/carnivores (Scott and Crossman, 1973; Eakins, 2014), although rock bass is thought to have a smaller range of prey sizes due to a smaller gape size (Mittelbach and Persson, 1998). A significant increase in the risk of extirpation of several small prey fishes following the establishment of rock bass was recently demonstrated in

Ontario lakes (Alofs and Jackson, 2015b). Rock bass may also be more active than smallmouth bass in winter (Scott and Crossman, 1973; Eakins, 2014), which could mean an extended temporal window for negative impacts beyond what has been described for smallmouth bass.

4.3. Potential loss of cold- and cool-water species, and Ontario's Far North as a climate refuge

Irrespective of any potential negative impacts of invading centrarchids on our focal native species, both cool-water walleye and cold-water lake whitefish are predicted to lose more than 75% of historically occupied lakes. Lake whitefish stand to lose the greatest proportion (83%) of historical populations, and losses are projected to occur throughout their historical Ontario range. Predicted losses are most intense in southern, central, and western Ontario, however loss is also very common throughout OFN. That said, OFN contains the greatest concentration of predicted maintenance of historical populations and a handful of new lake habitats. The situation is very similar for cool-water walleye south of OFN, where 80% of historical populations stand to be lost. However, OFN represents a potential stronghold for future hospitability, where there are only a few projected population losses countered by 183 maintained populations and 51 potential gains. Van Zuiden et al. (2016) similarly predicted high probabilities of occurrence for walleye and cold-water cisco across OFN, and very low probabilities of occurrence in south and central Ontario.

It is very difficult to know the timelines over which population losses may occur, due to the uncertainty of the predicted direct impacts of climate change and the potential indirect impacts of climate-mediated centrarchid invasions. Extinction debts (i.e., accumulations of delayed local extinctions) can accrue if insufficient time has passed for impacts to take effect on vulnerable populations (Kuussaari et al., 2009; Jackson and Sax, 2010). It is possible that some vulnerable populations may have the ability to adapt to climate change depending on rates of change, however in the case of northern cold-water specialist populations that have persisted in the same waters for centuries, adaptive potential may be limited (McDermid et al., 2012, 2013).

An important avenue for continued research will be to evaluate the extent to which OFN may serve as a climate change refuge for cool- and cold-water fishes such as lake whitefish and walleye. Climate and the interaction between climate and lake depth were two of the most important drivers of occupancy in our focal cool- and cold-water species, however the relative importance of local drivers and their interactions with climate conditions may vary among other species in these thermal guilds. Individual species will also vary in their respective ability to track climate suitability, based on traits such as dispersal ability, as well as the likelihood of intentional or unintentional movement by humans (Alofs et al., 2013). For instance, lake trout and cisco are both cold-water fishes with subsistence and recreational value, that have temperature preferences within the same range as lake whitefish, and may also share similar local habitat affiliations, such as a positive association with lake depth (Scott and Crossman, 1973; McDermid et al., 2015a; Van Zuiden et al., 2016). The modeling approach developed in this study can be used to make specific predictions for additional species and to evaluate the relative influence of climate and local lake characteristics on the occurrence of species within and among thermal guilds.

The disparity of lake characteristic data for OFN (Chu et al., 2005; Minns et al., 2008), particularly for Hudson Bay lowland lakes, means that we are unable to make local predictions of fish occupancy for the majority of northern lakes at this time. Van Zuiden et al. (2016) used their lake-level predictions to generate a smoothed probability of occurrence surface across un-sampled areas. However, this ignores the variability of important morphological characteristics among intervening un-sampled lakes, which will interact with climate to determine habitat suitability. Ideally, a field campaign to acquire physical and biological data in poorly represented watersheds would enable a more robust application of distribution models. However, given the logistical limitations around sampling in OFN, developing methods of remotely estimating lake characteristics such as maximum depth and water clarity would greatly improve research capacity. Advances in remote sensing technologies have enabled researchers to estimate turbidity and other water clarity metrics for individual or small groups of neighboring waters (Harrington et al., 1992; Ritchie et al., 2003). It may not be long before the capacity of these techniques is improved to enable estimations over broad regions (Politi et al., 2015). Also, because of the known relationships between the relative position of lakes in catchment networks, catchment topography, and local lake characteristics (i.e., size, trophic status; Sorrano et al., 1999), it may be possible in the future to use lake area and elevation data from remotely sensed data products to develop spatial interpolation models for maximum and secchi depths or basin shape.

Even with the currently patchy coverage of lake predictions across northern Ontario, these results provide a new lens through which conservation priorities for freshwater fishes can be considered. Conservation priority can be assigned to lakes that are predicted to continue to support historical cold- and cool-water species, as well as lakes that are predicted to become hospitable within watersheds where the species have occurred in the past. Any of these lakes likely to support the invasion of warm-water species could be de-prioritized, and remaining candidate lakes could then be assessed in more detail, using whole lake models to quantify the seasonal availability of cold- or cool-water habitats (Minns and Shuter, 2013).

Catchment level freshwater conservation planning has been recommended for boreal regions in the face of climate change (Schindler and Lee, 2010). Our model results could be used to rank the conservation value of whole catchments, based on the relative numbers of known historical populations, connectivity to neighboring catchments with historical source populations, and the predicted future availability of suitable lake habitat. Such analyses would be most valuable if paired with catchment-level risk assessments for the potential spread of rock bass and other warm-water invasives, which account for movement pathways.

4.4. General conclusions

Our analyses have shown that modified logistic species distribution models, trained using only a small set of candidate local environmental variables combined with indicators of human use intensity and climate conditions, can make accurate predictions of the historical and contemporary distributions of the three focal fish species selected for this study. This is an encouraging finding, given the stark lack of local lake attribute data at higher latitudes in Ontario and across Canada (Chu et al., 2005; Minns et al., 2008). It is our hope that by focusing future efforts toward filling in data gaps for the environmental variables used here, researchers could greatly enhance predictive capabilities in data poor areas with minimal effort. Modern GIS products have made it possible to obtain information on lake area and elevation in remote and un-sampled lakes, therefore the final hurdle lies in obtaining maximum depth and water clarity information for such waterbodies. Developing and testing techniques to estimate secchi and maximum lake depths or basin shape could greatly reduce field sampling efforts, which are extremely costly in the hard-to-access regions of the far north.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.08.006>.

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